Molecular origins of Redfield ratio and converges to N:P~16 due to evolution and upwelling.

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Short Abstract **— Among the biosphere's largest patterns is atomic nitrogen:phosphorus ratio (N:P) ~ 16 found throughout deep ocean [1]; though N:P of individual phytoplankton species ranges from 6 to 60, the average N:P of plankton is also ~16 [1,2]. Discovered empirically by Redfield 75 years ago [3,4], this pattern is central to carbon sequestration models and marine biogeochemical cycling [5,6]. However, the rationale behind N:P=16 is not known. Here, we show that Redfield stoichiometry follows from fundamental molecular values such as N in amino acids, N and P in nucleotides, and from cellular regulation of RNA and protein synthesis; in nutrient replete conditions N:P~16 reflects biochemically optimal RNA:protein. If nutrients are limiting, our nonlinear dynamic model shows how evolutionary stable strategy deviates cellular N:P from Redfield ratio. Finally, we show the role of Earth's rotation (that makes upwelling possible) on the convergence to Redfield ratio ~16 over geological times. Our work shows that Redfield N:P originates on a molecular scale while evolution coupled with Earth's rotation amplify the pattern to the global scale.**

Keywords **— Redfield ratio, RNA, protein, cell regulation, translation, transcription, evolution, plankton, ocean, multiple scales, pattern, convergence.**

I. Introduction

THE molecular foundation of life on the Earth - DNA, RNA, and proteins - is made of nucleotides and amino acids. Each amino acid requires N, and each nucleotide requires N and P. The demand for these elements on molecular scale not only manifests itself globally - N and P limit the world's primary productivity, but also exhibits absolute constancy throughout all life forms - exactly one P atom is in each nucleotide and a fixed number (1 to 5) of N atoms are in each nucleotide and amino acid. Can this numerical constancy of N:P in the building blocks of life manifest itself too on the global scale? Expressly, can it have its imprint throughout ocean basins, where N:P is nearly constant ~15 to 16?

II. Methods

We consider two fundamental attributes of RNAs and proteins: their elemental content and the rates of their synthesis. By considering cellular regulation of transcription and translation, we derive a formula for the optimal RNA:protein ratio. The formula yields N:P ~14-16 for both prokaryotes and eukaryotes in nutrient replete conditions. However, when we consider the effect of the environment and evolution in our ODE model, then evolutionary optimal N:P deviates from 16. The reconciliation of evolutionary and molecular optimums requires the consideration of upwelling, which is a result of Coriolis effect on Earth.

Though we illustrate our results with numerical simulations, we derive our core results analytically and show that they are robust to any particular choice of parameter values and growth functions.

III. Conclusion

We show that Redfield pattern arises as a self-regulatory mechanism rooted in multiple organizational scales: from synthesis of major biomolecules to competition and evolution of phytoplankton species to the effects of Earth's rotation on nutrient cycles. Thus, N:P~16 in oceans is not a historic accident, but a number that stems from the structure of RNAs and proteins, evolutionary forces, and peculiarities of nutrient flows in oceans.

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